

**TAXONOMY OF *ACIURINA TRIXA* CURRAN (DIPTERA: TEPHRITIDAE)
AND ITS LIFE HISTORY ON *CHRYSOTHAMNUS NAUSEOSUS* (PALLAS)
BRITTON IN SOUTHERN CALIFORNIA; WITH NOTES ON
A. BIGELOVIAE (COCKERELL)**

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Abstract.—*Aciurina trixa* Curran is reinstated as a valid taxon and distinguished from *A. bigeloviae* (Cockerell) with which it had been synonymized. The immature stages of *A. trixa* also are described in detail. This tephritid is univoltine and monophagous on *Chrysothamnus nauseosus* (Pallas) Britton. Adults emerge in early spring and lay eggs singly in axillary buds on the current season's branches. First instars eclose in ca. 1 week and tunnel basipetally along a vascular trace into a branch. Gall growth begins during the first larval stadium and continues through the spring and summer. Gall growth was complete by late fall when most branch tunnels and galls contain second instars. Second instars continue to feed in the branch tunnels and begin excavating the gall lumen. Larval growth proceeds through the fall, and by December most galls contain third instars. Third instars confined most of their feeding to the gall, typically filling the branch tunnel with packed frass. Puparia were first observed in mid-February. Pupariation took place within the gall lumen and lasted ca. 2 weeks. Adult females were proovigenic and mated shortly after emergence and repeatedly.

Key Words: Insecta, *Aciurina* taxonomy, immature stages, galls, oviposition behavior, parasitoids

Aciurina trixa Curran is reinstated as a valid species, the immature stages are described for the first time, and a redescription of the adult is provided. The biology, oviposition behavior, distribution, and natural enemies of *A. trixa* are also described for populations occurring in southern California.

MATERIALS AND METHODS

Our field studies of the biology of *A. trixa* were conducted between 1989 and 1994 in southern California. Our primary study and collection locations were Los Angeles County, Pearblossom at ca. 830 m; San Bernardino Co., Cajon Junction at ca. 1000 m, and Pioneertown at ca. 1200 m.

Field studies of adult behaviors were conducted at the Cajon Junction site during the spring of 1990–1992 on *C. nauseosus*. Field data were supplemented by laboratory dissections, measurements, and photography of infested host-plant material, and subsequent rearing of adults and their parasitoids.

Twenty-three ova were obtained for study by dissection of gravid, field-collected females. Five first, 20 second, and 18 third instar larvae and two puparia were dissected from infested *C. nauseosus* and all immature stages were examined using scanning electron microscopy (SEM). All specimens for SEM were fixed in 70% EtOH, rehydrated to distilled water in a de-

creasing series of acidulated EtOH, post-fixed in 2% aqueous osmium tetroxide for 24 h, dehydrated to absolute EtOH in an increasing series of EtOH dilutions, critical-point dried, mounted on stubs, sputter-coated with a gold-palladium alloy and examined on a JEOL JSM C35 scanning electron microscope in the Department of Nematology, University of California, Riverside. Micrographs were prepared on Polaroid P/N 55 film at 15 kV accelerating voltage.

Tephritid names follow Foote et al. (1993), except where amended below; larval terminology follows Headrick and Goeden (1991) and Goeden and Teerink (1996a, b, c); terms for adult behaviors follows Headrick and Goeden (1994); and plant names follow Munz (1968, 1974) and Munz and Keck (1959). Abbreviations used as follows: AMNH—American Museum of Natural History; CAS—California Academy of Sciences; CDFa—California Department of Food and Agriculture; UIM—University of Idaho, Moscow; UCR—University of California, Riverside; WSUP—Washington State University, Pullman. Voucher specimens of adult *A. trixa* and its parasitoids reside in the research collection of RDG. Preserved immature stages are held in the research collection of JAT. Means \pm standard errors are provided throughout.

RESULTS AND DISCUSSION

TAXONOMY

The taxonomy of *Aciurina* species occurring in the western United States has had a tortuous history. Unclear or unknown host-plant associations, variable gall morphology, incorrect insect gall-former attributions, and the recently discovered regional sexual dimorphisms (Goeden and Teerink 1996b, c) have all contributed to the difficulty of elucidating the species comprising this genus. Based on our extensive collections of reared material and examination of museum specimens, many taxonomic issues have recently been clarified (Goeden and Teerink 1996a, b, c).

Although, *A. trixa* has been mentioned in the literature subsequent to its synonymization with *Aciurina bigeloviae* (Cockerell), no formal resurrection of this species has been published. Most recently, notes on the biology, gall formation, and sexual behavior of *A. trixa* were reported from northern Arizona by Fernandez and Price (1994), who cited the work of Dodson and George (1986) for identification of the species that they studied. Foote et al. (1993) remarked that the names synonymized by Steyskal (1984) and Norrbom (1989) were available.

Adult.—Curran (1932) erected the genus *Aciurina* and designated the type species as *A. trixa*. Steyskal (1984) revised the genus and synonymized *A. semilucida* (Bates) (1935) and *A. trixa* with *A. bigeloviae* (Cockerell). Recently, Goeden and Teerink (1996c) resurrected *A. semilucida* based on the discovery of sexually dimorphic wing patterns among disparate populations theretofore unrecognized. This discovery was based primarily on examination of flies individually reared from known galls which reconfirmed the separate species status of *A. semilucida*. Similarly, Dodson and George (1986) provided biological, behavioral, and genetic evidence that *A. trixa* was distinct from *A. bigeloviae* based on flies individually reared from known galls from throughout the southwestern U.S., excluding southern California, but they did not formally resurrect the former species. Our examination of material, reared or otherwise collected, in southern California and museum specimens from all states west of the Rockies, except Oregon, provides more pieces of the puzzle concerning the taxonomic status of *A. trixa*.

The following description supplements the original description of Curran (1932), with characters since recognized as important in separating *Aciurina* species (Steyskal 1984, Foote et al. 1993).

Aciurina trixa Curran (Fig. 6I)

Female holotype. Head.—White to golden; antenna golden, arista lighter basally,

darker apically; bristles as in original description; all uniformly concolorous with head basally, but dark apically.

Thorax.—Dark gray, with uniform covering of gray pollinosity, setulae white. Bristles as given in original description, their location as given in Foote et al. (1993). Scutellum dark brown with posterior apex lighter. Coxae and legs golden; fore-coxa with patch of very fine setae anteriorly; forefemur thickened dorsally, with 2–3 rows of short stout setae, a ventrolateral row of longer setae extending entire length of femora, and at most a single incomplete row of dark setae ventrally (see male description). Wing mostly dark brown with marginal hyaline incisions and internal markings as illustrated by Curran (1932 Fig. 5) (see below for variations). Pterostigma with a proximal hyaline incision; hyaline spot in cell br round; cell cua₁ with 1 large and 2 small marginal hyaline incisions, larger one includes anal lobe; cell m with 2 marginal hyaline incisions, distal incision extends into cell r₄₊₅, often touching vein R₄₊₅.

Abdomen.—Shiny, reddish brown, sparsely covered with very fine yellow bristles, tergite 6 darker, at least in patches, than preceding segments; syntergosternite 7 fuscous to black; aculeus (visible in type) lanceolate without distinct markings or indentations.

Male. Head.—White to golden, vertex darker, ocellar triangle dark; bristles stout, golden; antenna golden, arista golden basally, dark apically.

Thorax.—Dark, fine gray pollinose, setulae short white, dorsocentral seta nearer to postsutural supralar seta than in female; legs golden; fore coxa with anterior patch of fine setae; forefemur thickened, much larger than in remaining legs, larger than female forefemur relative to sizes in remaining legs; rows of stout setae dorsally, ventrolateral row of larger setae extending entire length of femur; ventrally 2–3 rows of short dark setae (possibly aid in securing hold on female during copulation [Dodson

1987]). Wing with marginal hyaline incisions and internal markings similar to that of female (see variations below).

Abdomen.—Brown with darker markings anteriorly, dark around lateral margins, tergite 1 almost completely dark, tergite 5 dark laterally; post-abdomen dark, surstyli golden, prenisetae dark.

Variation.—In males, the head color varies from golden to brown. The setulae of the thorax in both sexes are white or orange. Variation in setulae color among populations of flies was not observed; most specimens, including the holotype of *A. trixa*, have the white form. In California, the specimens reared from small galls all have orange setulae. The thorax color in both sexes varies from light brown to nearly black.

The wing markings varied among the specimens examined. The hyaline or subhyaline incision on the proximal side of the pterostigma can be quite faint among the specimens reared from California. This was also observed among specimens collected (swept or reared) from Idaho. The individuals reared from small galls in southern California were darker than those reared from the larger galls and the infuscation of their wings was heavy. However, even in these flies, a faint mark on the proximal side of the pterostigma was observed, especially on or near the costal vein. The hyaline spot in cell br varies from circular to oblong in *A. trixa*. Only very rarely will specimens (both sexes) have a small infuscation on the wing margin within the proximal hyaline mark in cell m, but it is not elongate and never complete (i.e. bridging the infuscation, thereby forming 2 hyaline incisions from the proximal hyaline mark). In cell c the infuscation can be either narrow or wide with the widest marking being nearly equal in width to the distance between vein S_c and R₁. In approximately 1/3 of the female specimens examined, the wings have three hyaline marks in cell r₁ like *A. trilitura* Blanc and Foote, with only the distal mark either present or absent. Cell

cua₁ typically has 2 small hyaline markings distally and a larger one proximally. The distal hyaline mark in cell m is sometimes constricted at vein M; in a few specimens the constriction is complete and separates the mark in cell m from the mark in cell r₄₊₅. The hyaline mark in cell r₄₊₅ can also be constricted and thus bilobed. The mark touches vein R₄₊₅ in about half of the specimens examined. In 3 specimens examined, the hyaline mark in cell r₄₊₅ is completely constricted forming 2 distinct marks.

Material examined.—*Aciurina trixa*: Female holotype, UTAH: Stansbury I., 13.vi.13 (AMNH). CALIFORNIA: Inyo Co., Grapevine Canyon, 2 males 1 female, 20.v.1988, (R. D. Goeden) (UCR); Lone Pine, 1 male, no gall, 1.vi.1937, (E. P. Van Duzee) (CAS). Kern Co., Cane Brake Valley, W. Side Walker Pass, 3,000 ft., 1 female and 1 male with gall, 1 female without gall, *Chrysothamnus nauseosus*, 9.xi.70, (J. T. Howell) (CAS); Spanish Needle Creek, 3 females with galls, 6 males with galls, 11.iv.1989, (R. D. Goeden) (UCR); Walker Pass, 1 male with gall, 11.iv.1989, (R. D. Goeden) (UCR). Los Angeles Co., Pearblossom, 7 males with galls, 5 females with galls, 18.ii.1987, (R. D. Goeden) (UCR). Maricopa, Co., 9 females, 2 males, 31.iii.1931, (E. P. VanDuzee) (CAS). San Bernardino, Co., Barstow, 1 female, "Ex. *Artemisia*", 16.iv.1938, (T. G. H. Aitken) (CAS); Forest Falls, 7 females with galls, 2 males with galls, 3.v.1988, (R. D. Goeden) (UCR). San Luis Obispo Co., Maricopa Grade, 4 males with galls, 3 females with galls, 21.iii.1931, (E. P. VanDuzee) (CAS). Santa Barbara Co., Ventucopa, 2 females with galls, 25.iii.1959, (R. P. Allen) (CDFA). COLORADO: Grand Junction, 1 female, 20.vi.01, (WSUP). Salida, 28.vi.1933, 3 females 3 males, "ex *Chrysothamnus*", (Cockerell) (WSUP). IDAHO: All with galls: Bear Lake Co., Dingle, 1 female, 17.vi.1975, (J. T. Wangberg) (UIM). Boise Co., Horseshoe Bend, 3 females, 21.v.1975, (J. T. Wangberg) (UIM). Box Elder Co., Strevell, 1 male, "*C. nau-*

seosus", 19.iii.1974, (J. T. Wangberg) (UIM). Butte Co., Howe, 2 males, "*C. nauseosus*", 27.iii.67, (E. J. Allen) (UIM). Franklin Co., Preston, 1 male, 18.iii.1974, (J. T. Wangberg) (UIM). Idaho Co., Lucille, 1 male, 2 females, 12.iv.1975; 2 males, 24.iii.1974; 2 females, 28.iv.1974, (Wangberg) (UIM); Riggins, 1 female, 29.iv.1974, (J. T. Wangberg) (UIM); Slate Creek, 1 male, 20.v.1975, (J. T. Wangberg) (UIM). Lemhi Co., Leadore, 1 female, 2 males, 21.vi.1975, (J. T. Wangberg) (UIM). Oneida Co., Stone, 1 female, "*C. nauseosus*", 19.iii.1974, (J. T. Wangberg) (UIM). Owyhee Co., Walters Ferry, "*C. nauseosus*", 5 females, 3 males, 31.iii.1967, (E. J. Allen) (UIM). Bruneau, 1 female, 26.vi.1974, (J. T. Wangberg) (UIM). Twin Falls Co., Twin Falls, 1 female, 29.iii.1967, (E. J. Allen) (UIM). NEVADA: Washoe Co., Hills just N. of Sparks, 1 male, 1 female, 1 gall, (J. T. Howell) (CAS). NEW MEXICO: Santa Fe, 2 males, 21.vi.1926, (E. C. VanDyke) (CAS). UTAH: Provo, 1 female, 1.v.1963, (WSUP). Female Paratype: Collinston, 21.vii.1927, "Det. Curran" (G. F. Knowlton) (AMNH). WASHINGTON: Okanogah Co., 1 female, no gall, 19.v.1968, (WSUP). Whitman Co., Steptoe Cyn., 1 female, no gall, 17.v.1973, (WSUP).

Aciurina bigeloviae. ARIZONA: Flagstaff, 1 male, no gall, 28.vi.1971, (E. Klee) (CAS). NEVADA: Reno, 1 female with gall, 9.v.1891, (F. Hilman) (CAS).

Diagnosis—*Aciurina trixa* is variable in its adult morphology and the morphology of the galls it induces on its host plant, *Chrysothamnus nauseosus*. *Aciurina trixa* can be distinguished from its closest relative, *A. bigeloviae*, based primarily on gall type, and for the majority of specimens by the presence of a hyaline mark on the proximal side of the pterostigma and by the absence of an elongate or dividing mark within the proximal hyaline spot in cell m, [see also Fig. 1 in Dodson and George (1986)]. This distinction makes *A. bigeloviae* a rare species known only from large cottony galls and restricts its range to exclude Cal-

ifornia. However, one record indicates its range may extend into northeastern California along the edge of the Great Basin (Foote and Blanc 1963).

Aciurina trixa differs from *A. semilucida* by having multiple hyaline spots in cell r_{2+3} (cf. Goeden and Teerink [1996c], Fig. 1A–E) or from females of *A. semilucida* occurring in California by not having the distal hyaline spot in cell m extend beyond vein R_{4+5} into cell r_{2+3} (cf. Goeden and Teerink [1996c], Fig. 1F). *Aciurina semilucida* is known to form galls on *Chrysothamnus viscidiflorus* (Hooker) Nuttall and *C. nauseosus* (Foote et al. 1993). *Aciurina semilucida* galls are readily distinguishable from galls of *A. bigeloviae* and *A. trixa* by being light green, pyriform with an attenuated apex, covered with a uniform, light-colored pubescence, and bearing several basal leaves (Goeden and Teerink 1996c).

Both *A. trixa* and *A. bigeloviae* are known only from *C. nauseosus*; however, the galls they induce are readily distinguishable and is the best character for species recognition. *Aciurina bigeloviae* is known to form only large, cottony galls [see also Dodson and George (1986), Figure 2B] that sometimes bear small leaves studding the gall body, rather than a rosette of basal leaves as in *A. semilucida* (Goeden and Teerink 1996c). The tomentum of *A. bigeloviae* galls is thick and continuous over the entire gall, appearing like a wad of cotton. *Aciurina bigeloviae* galls have been collected from several sites in Idaho, Colorado, Arizona, New Mexico and Utah; however, most specimens in collections do not have the galls from which they were reared. The galls of *A. maculata* (Cole) also occur on *C. nauseosus* and are cottony; however, they are much smaller than *A. bigeloviae* galls and the adults are readily distinguishable (Foote et al. 1993).

No cottony tephritid galls have ever been found on *C. nauseosus* in southern California (RDG, unpublished data). The galls of *A. trixa* vary in external morphology throughout its range. At present we can dis-

tinguish two types of galls in southern California. There are reportedly three gall forms in Idaho (Wangberg 1981). Galls in southern California have a waxy or resinous outer layer. The most common whitish (pearly) gall found in California is shown in Fig. 6B. The smaller, brownish gall has a more restricted distribution, occurring on the north slope of the San Bernardino Mountains bordering the Mojave Desert (shown dissected in Fig. 6G, H).

The key to species of *Aciurina* as given in Foote et al. 1993 is modified to include the resurrection of *A. trixa* (figures cited are from Foote et al. 1993, except as noted).

- 10. Pterostigma along costa no more than 1.5 times as long as its greatest width (Fig. 121, c); vein dm-cu nearly straight (Fig. 121, e), the lower apical angle of cell dm about 65° (Fig. 121, f); wing predominantly hyaline *notata* (Coquillett)
- Pterostigma along costa at least 2.0 times as long as its greatest width (Fig. 124, a); vein dm-cu usually bowed apicad (Fig. 124, b), the lower apical angle of cell dm seldom less than 90° (Fig. 124, c); wing patterned 11
- 11. Galls without tomentum; pterostigma of at least one wing with a proximal hyaline or subhyaline incision (can be very faint and only on and slightly extending from costa) (Fig. 124; Dodson and George, Fig. 1c); proximal marginal hyaline incision in cell m usually lacking median, dark mark . . . *trixa* Curran
- Galls with cottony tomentum, pterostigma and costa dark from Sc to R_1 in most specimens (Fig. 122, b); proximal marginal hyaline incision in cell m usually with a median, dark, often elongate mark (Fig. 122), which sometimes divides the incision (Steyskal 1984, Fig. 13) (Dodson and George 1986; Fig. 1a, b, d) *bigeloviae* (Cockerell)

Immature stages. Egg.—White, elongate-cylindrical with narrow, parallel-sided, short pedicel and bluntly rounded, basal end (Fig. 1A). Pedicel with ring of multipored aeropyles and micropyle at apex (Fig. 1B). Chorion with slightly elevated striations on pedicel.

First instar.—Translucent white, globose, bluntly rounded anteriorly and posteriorly, three to four rows of acanthae circumscribe



Fig. 1. Egg of *Aciurina trixa*. (A) Habitus; (B) pedicel.

the body at intersegmental lines, lateral midline with up to four rows of acanthae (Fig. 2A). Gnathocephalon conical, rugose pads absent (Fig. 2B). Mouth hook with two teeth (Fig. 2B-1), cushioned by an integumental petal (Fig. 2B-3), median oral lobe present (Fig. 2B-2). Anterior sensory lobe with four sensory organs (Fig. 2B-4), dorsal sensory organ comprised of single papilla (Fig. 2B-5). Stomal sense organ laterad of mouth lumen bearing sensory papillae (Fig. 2B-6). Posterior spiracular plates contiguous, rounded, and protruding; each plate bears two rimae (Fig. 2C-1) and typically four, spine-like, interspiracular processes (Fig. 2C-2). Compound sensilla ventrad of spiracle each comprised of two stelex sensilla (Fig. 2C-3).



Fig. 2. First instar of *A. trixa*. (A) Habitus, anterior to left; (B) gnathocephalon, lateral view, 1—mouth-hooks, 2—median oral lobe, 3—integumental petal, 4—anterior sensory lobe, 5—dorsal sensory organ, 6—stomal sense organ; (C) caudal segment, 1—rima, 2—interspiracular process, 3—compound sensilla.

Second instar.—White, oblong-elliptical, bluntly rounded anteriorly and posteriorly,

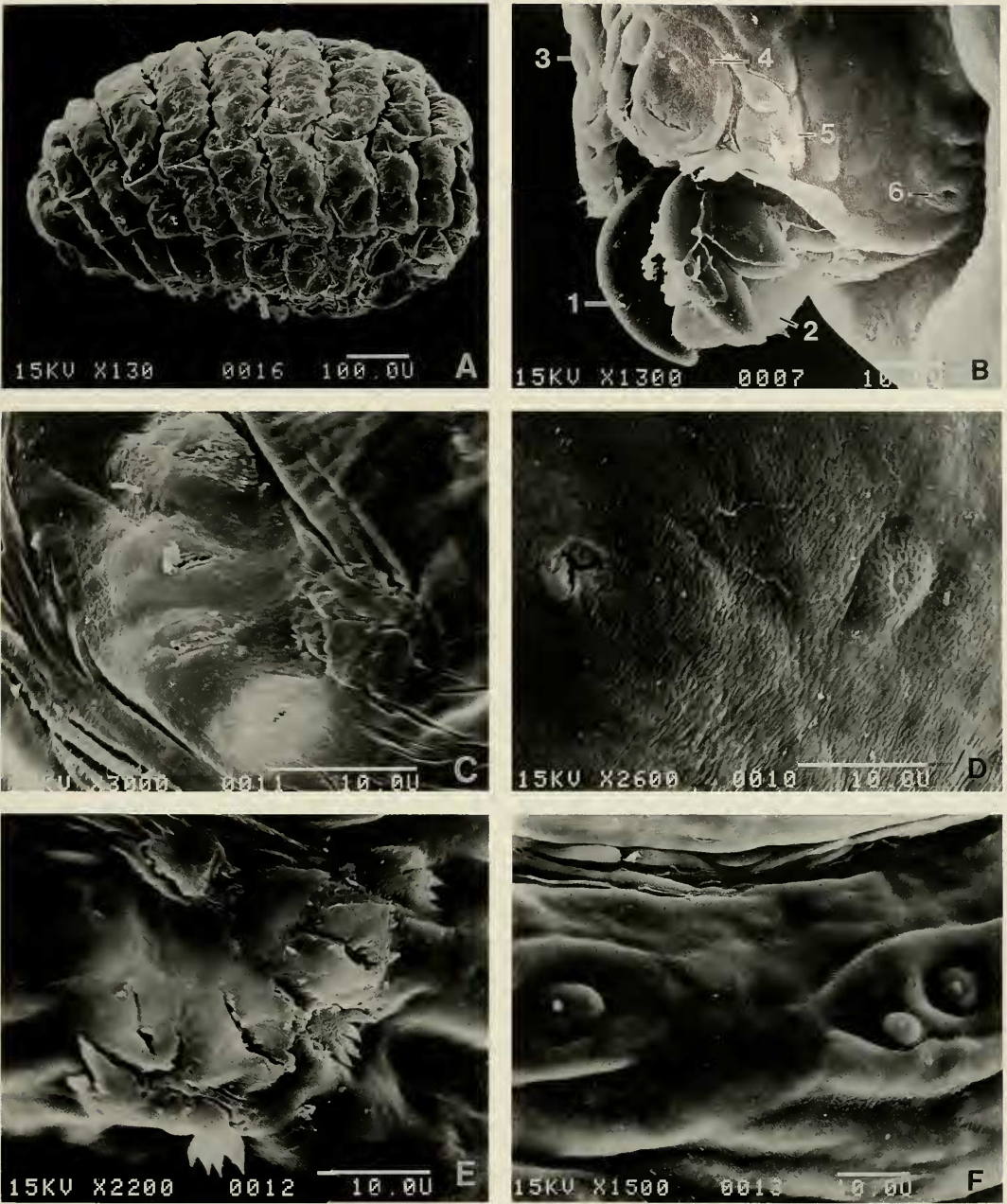


Fig. 3. Second instar of *A. trixa*. (A) Habitus, anterior to left; (B) gnathocephalon, lateral view, 1—mouth-hook, 2—median oral lobe, 3—dorsal sensory organ, 4—anterior sensory lobe, 5—stomal sense organ, 6—lateral sensory organ; (C) anterior prothoracic spiracle; (D) lateral spiracular complex, spiracle to left, (E) posterior spiracular plate; (F) compound sensilla.

several rows of acanthae circumscribe the body at intersegmental lines (Fig. 3A). Gnathocephalon conical, smooth, except for rugose pads surrounding stomal sense or-

gan. Mouth hooks bidentate (Fig. 3B-1), median oral lobe rounded anteriorly, fleshy ventral lobe attached basally to the labial lobe (Fig. 3B-2). Dorsal sensory organ

comprised of single papilla (Fig. 3B-3), anterior sensory lobe with four sensory organs (Fig. 3B-4), stomal sense organ with three to five sensilla (Fig. 3B-5), lateral sensillum with single verruciform papilla (Fig. 3B-6). Prothorax smooth, anterior thoracic spiracle with three to four papillae (Fig. 3C). Lateral spiracular complex on mesothorax with one spiracle and two verruciform sensilla; metathorax and abdominal segments I–VII with one spiracle and one verruciform sensillum (Fig. 3D). Posterior spiracular plate with three rimae and four, single or multi-branched, interspiracular processes (Fig. 3E). Compound sensilla comprised of two stelex sensilla (Fig. 3F).

Third instar.—White, oblong-elliptical, bluntly rounded on both ends, acanthae restricted to area around intersegmental lines (Fig. 4A). Mouth hooks bidentate (Fig. 4B-1), median oral lobe with numerous fleshy protuberances on ventral lobe, attached basally to labial lobe (Fig. 4B-2). Gnathocephalon smooth, with rugose pads laterally and ventrally near mouth lumen (Fig. 4B). Dorsal sensory organ with a single papilla (Fig. 4C-1), anterior sensory lobe with four sensory organs (Fig. 4C-black lines), stomal sense organ invested with sensoria (Fig. 4C-2). Prothorax smooth, anterior thoracic spiracle with three to four non-protruding papillae, each with a single slit, ecdysial scar visible (Fig. 4D). Lateral spiracular complex with single spiracle and verruciform sensillum (Fig. 4E). Posterior spiracular plate with three rimae, and reduced interspiracular processes (Fig. 4F). Compound sensilla nearly contiguous, each with two reduced stelex sensilla.

Puparium.—Shiny; dark fuscous to black, some with lighter brown around the middle; elongate-reinform, bluntly rounded on both ends, 4.0 ± 0.1 (3.1–4.3, $n = 9$) mm long and 2.0 ± 0.1 (1.7–2.2, $n = 8$) mm wide (Fig. 5A). Anterior end with invagination scar and anterior thoracic spiracle (Fig. 5B); posterior end with spiracular plates non-protruding (Fig. 5C).

Diagnosis.—The immature stages of *Aci-*

urina thoracica Curran (Headrick and Goeden 1993), *A. ferruginea* (Doane) and *A. michaeli* Goeden (Goeden and Teerink 1996a), *A. idahoensis* Steyskal (Goeden and Teerink 1996b), and *A. semilucida* (Bates) (Goeden and Teerink 1996c) have been described in detail. *Aciurina trixa* is the last, described California species of *Aciurina* to be examined by us. The egg of *A. trixa* is smooth, nearly parallel-sided, with a pedicel ca. 0.015 mm in length. The eggs of *A. ferruginea*, *A. michaeli*, *A. idahoensis* and *A. semilucida* have elongate pedicels; the pedicel of the latter being ca. half as long as the other species with elongate pedicels. The egg of *A. thoracica* has a short pedicel and heavy reticulation on the pedicel end that diminishes to a smooth surface near the midpoint of the egg body.

The third instars of *A. michaeli* and *A. semilucida* have abdominal segments III–V expanded dorsally producing an “ambulatory hump.” No other *Aciurina* species in California have this feature. The integument of *A. trixa* has minute acanthae restricted to the areas around the intersegmental lines; however, *A. thoracica* has acanthae in patches between the intersegmental lines. *Aciurina idahoensis*, *A. semilucida* and *A. ferruginea* have acanthae restricted to the ventral surface, and *A. michaeli* has acanthae ventrally and laterally.

The number of sensilla associated with the lateral spiracular complexes on the meso- and metathorax and abdominal segments I–VII (= sensilla formula) differs among the *Aciurina* species studied. The sensilla formula, i.e. the number of lateral spiracular sensilla on the mesothorax, the metathorax, and the abdominal segments (a ‘?’ indicates we were unable to locate the sensilla), for *A. michaeli* is 1, 1, 0; for *A. ferruginea* is 3, 3, ?; for *A. thoracica* is ?, 1, 1; for *A. idahoensis* is ?, 1, 0; for *A. semilucida* is 2, 2, 1; and for *A. trixa* is 2, 1, 1. The anterior prothoracic spiracles differ in the number of papillae among the species studied. *A. michaeli* has 3–4, *A. ferruginea* has 5, *A. thoracica* has 4, *A. ida-*

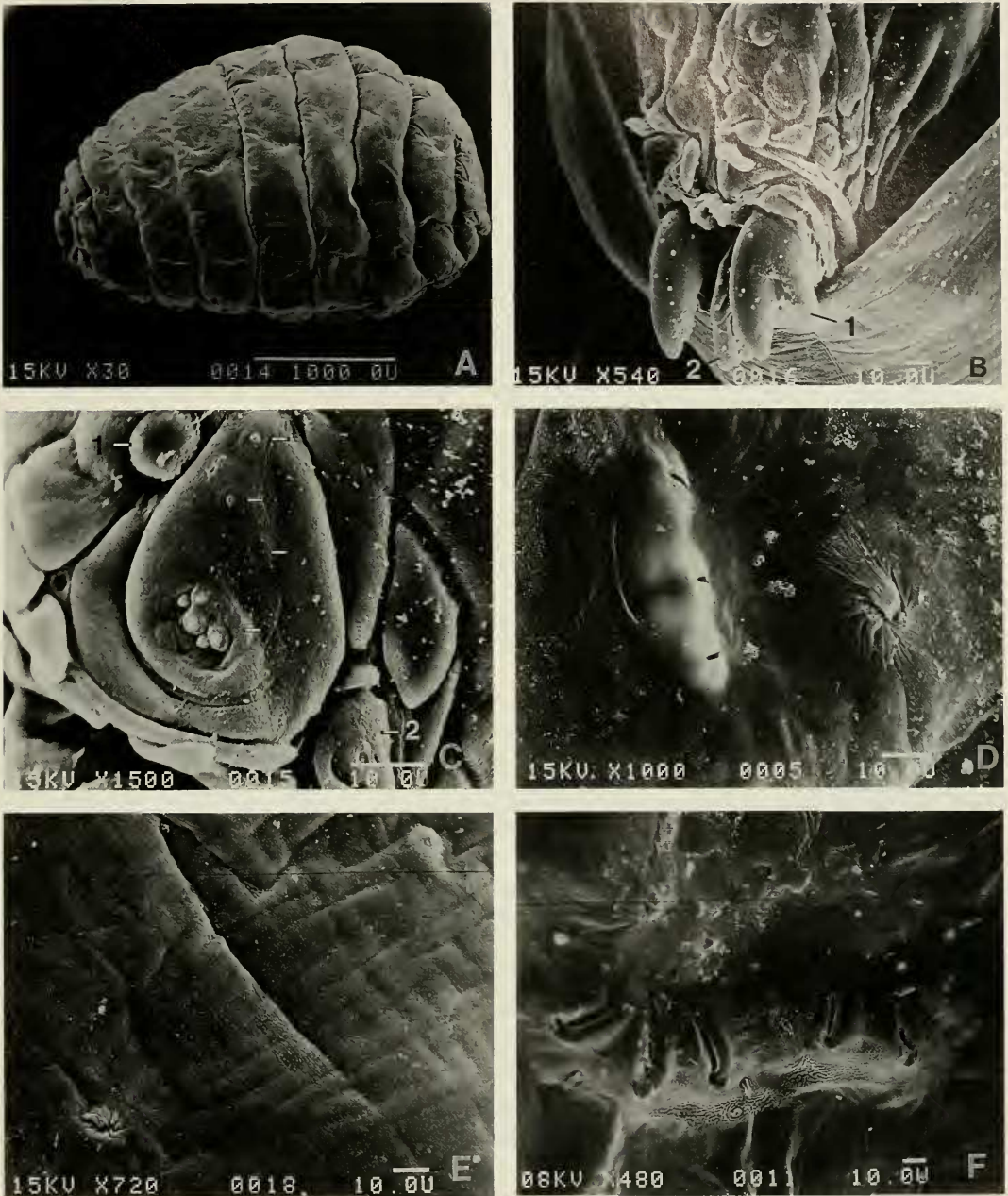


Fig. 4. Third instar of *A. trixa*. (A) Habitus, anterior to left; (B) gnathocephalon, anterior view, 1—mouth-hook, 2—median oral lobe; (C) sensory structures of the gnathocephalon, 1—dorsal sensory organ, 2—stomal sensory organ; (D) anterior prothoracic spiracle; (E) lateral spiracular complex, spiracle on left; (F) caudal segment with posterior spiracular plates.



Fig. 5. Puparium of *A. trixa*. (A) Habitus, anterior to left; (B) anterior invagination scar; (C) posterior spiracular plates.

hoensis has 3–5, *A. semilucida* has 3, and *A. trixa* has 4 non-protruding papillae. The first and second instars, and the puparia do not differ significantly in their morphology among the species studied in California.

BIOLOGY

Egg.—The eggs of *A. trixa* were laid singly into axillary buds on the current season's branches (Fig. 6A) soon after adult emergence in the spring in southern California (Table 1). The eggs were inserted partially into the tissues or among and parallel to the bud scales leaving the pedicel-bearing ends exposed. Eclosion occurred within 1 week after oviposition. The embryo turned 180° and the first instar exited basally, directly into the plant tissues.

Dodson (1987) reported that *A. trixa* females in New Mexico also laid eggs singly in axillary buds of *C. nauseosus* with galls becoming visible in August. Fernandez and Price (1994) reported that oviposition occurred in the field between late April and mid-August in northern Arizona and that eggs were laid singly in axillary buds.

First instar.—The first instar tunneled into the axillary bud tissues and continued down the vascular trace into the branch basipetally in the phloem between the epidermis and cambium. The feeding of the first instar stimulated the phloem and epidermis outside of the woody vascular cylinder surrounding the pith to expand, which resulted in the branch swelling at and near the axillary bud. Branch swelling was rapid and ceased when the first larval stadium ended. Branch swelling was also reported by Fernandez and Price (1994). Branch tunnel feeding concurrent with gall growth was also reported by Dodson (1987) and Fernandez and Price (1994).

The bud scales remained as small swellings at the base of galls. Gall growth continued through the spring and summer (April–September, Table 1) as the first instar excavated its tunnel within the branch from the base of the axillary bud basipetally. Thus, gall growth appeared to begin and proceed even though no larval feeding took place directly within the gall. Branch tunnels containing first instars averaged 3.1 ± 0.3 (range, 2.7–3.6; $n = 3$) mm long. Galls associated with branch tunnels containing

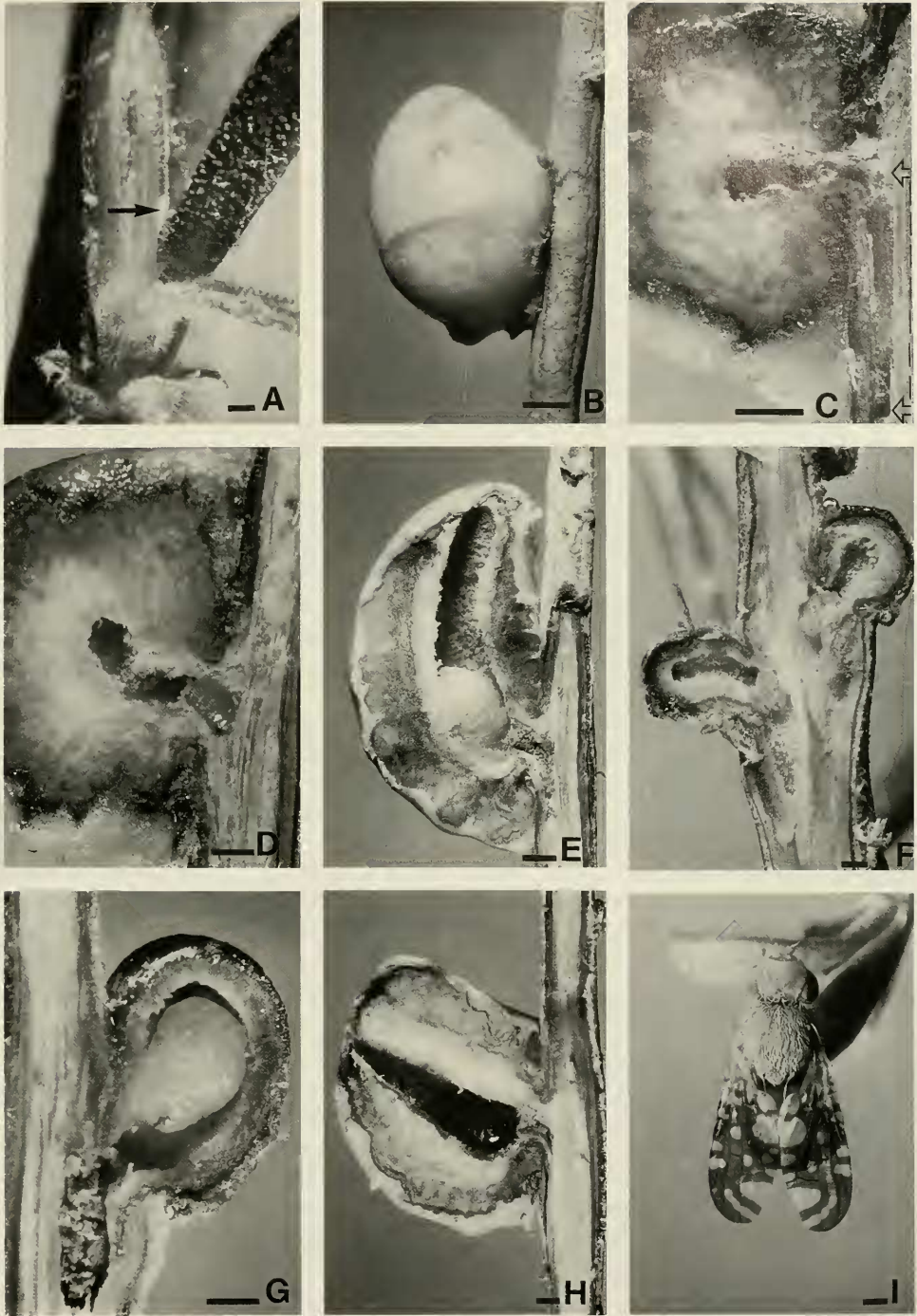


Fig. 6. Life stages of *A. trixa*. (A) egg inserted between leaf primordia (arrow); (B) mature gall, large, smooth, pearly, gall-type; (C) second instar feeding tunnel (arrows indicate beginning and end of tunnel) and partially excavated gall cavity; (D) second instar feeding in gall cavity and branch tunnel; (E) third instar in gall with exit tunnel formed apically and branch tunnel packed with frass; (F) second instars in small type of galls; (G) third instar in small gall-type; (H) puparium within gall locule, with anterior end facing exit window; (I) adult female of *A. trixa*. Bars indicate ca. 1 mm.

Table 1. Phenological development of *Aciurina trixa* on *Chrysothamnus nauseosus* in southern California. i—first instar; ii—second instar; iii—third instar.

		Month												
Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb			
eggs	eggs													
	i	i	i	i	i	i	i							
						ii	ii	ii	ii	ii	ii			
								iii	iii	iii				
adult	adult												iii	puparium

first instars measured 3.3 ± 0.2 (range, 2.8–3.6; $n = 6$) mm in diameter. First instars confined most of their feeding to the branch tunnel, as was also reported by Fernandez and Price (1994). Although galls were nearly full-size by the end of the first stadium in September or October (Table 1, Fig. 6B), gall locule excavation was begun only by the late first instars. This too, is consistent with the findings of Dodson (1987) and Fernandez and Price (1994). Gall locules averaged 0.96 ± 0.03 (range, 0.9–1.0; $n = 3$) mm wide.

Second instar.—By late October/early November gall growth was complete (Table 1). Dodson (1987) and Fernandez and Price (1994) also reported that gall growth was complete by November in New Mexico and Arizona, respectively. Galls containing second instars averaged 3.4 ± 0.07 (range, 2.3–4.1; $n = 31$) mm in diameter. The second instar continued to feed within the branch tunnel, enlarging it and extending its length basipetally (Fig 6C). Branch tunnels containing second instars averaged 3.3 ± 0.15 (range, 2.0–6.0; $n = 28$) mm long. The second instar also moved from the branch tunnel into the fully-formed gall and began excavating the gall lumen (Fig. 6D). The swelling around the branch tunnel did not increase with the continued feeding of the second instar.

As the gall lumen was enlarged, the inner walls became smooth; however, a substantial amount of parenchymatous tissue remained. Lumens of 28 galls containing second instars averaged 1.3 ± 0.08 (range,

0.5–2.5) mm wide and 3.16 ± 0.3 (range, 1.6–4.3) mm long. Frass accumulated within the gall lumen and in the branch tunnel as feeding continued. Frass was moved into the tunnel from the gall and packed into the basal end of the tunnel. The cast exuviae and cephalopharyngeal skeletons of first instars also were found within the packed frass. One late-second instar was observed beginning to form the exit tunnel in the gall, evidenced as a narrow tunnel toward the apex of the gall.

Third instar.—Larval growth proceeded through the fall, and by December most galls contained third instars (Table 1). Seventy galls containing third instars averaged 3.8 ± 0.06 (range, 2.6–5.0) mm in diameter. After the second molt, the third instars confined most of their feeding inside the gall, and the branch tunnel was used for frass storage (Fig. 6E). The gall walls were reduced in thickness by the feeding of the third instar. Lumens of 65 galls containing third instars averaged 2.3 ± 0.07 (range, 1.1–3.7) mm wide and 3.8 ± 0.07 (range, 2.5–5.4) mm long.

Third instars completed the exit tunnel by excavating up to the epidermis to form a circular window for adult emergence (Fig. 6E). The formation of exit tunnels by third instars was also reported by Dodson (1987) and Fernandez and Price (1994). Most windows were formed at or near the apices of galls.

Larval development and feeding, gall formation and growth, and phenological development were similar for both gall types

occurring in southern California (Fig. 6F, G). The smaller gall type has not been reported to occur outside of southern California (Dodson 1987, Fernandez and Price 1994).

Puparium.—Puparia were first observed beginning in mid-February and the puparial stage lasted ca. 2 weeks (Table 1). The puparium was formed in the lumen of the gall (Fig. 6H); no puparium was observed in a branch tunnel. The cephalic end of the puparium was oriented toward the window.

Adult.—Adults (Fig 6I) are circumnata (Headrick and Goeden 1994) and emerged in early spring (March–April, Table 1) following winter rainfall. Males were protandrous and awaited female emergence by perching near galls. Males lived an average of 32.1 ± 4.0 (range, 3–57; $n = 18$) days; females lived an average of 28.0 ± 5.3 (range, 13–43; $n = 6$) days. Courtship and mating behavior will be described and analyzed in a separate paper.

Females are proovigenic and emerge with a full complement of eggs. Mating was observed in the field when females were still teneral and was repeated throughout their lifetimes. Oviposition behavior was distinctive. Females walked or flew to the base of a branch and then walked towards its apex. At or near the top of the branch, they then turned and walked down the branch. At the first axillary bud, they stopped and probed with the oviscapae bent downward and extruded the aculeus. If the site was suitable, a female oviposited a single egg after extending the aculeus into the bud, either piercing the bud tissues or inserting the egg between the leaf primordia. After oviposition, females groomed, then moved downward to the next axillary bud and repeated this procedure. Females did not lay eggs into every axillary bud probed. Females continued basipetally in this manner until the base of the branch was reached, and then either walked or flew to another branch. Males stalked ovipositing females and attempted and usually success-

fully mated with them at any point during the above oviposition sequence.

Natural enemies.—The following were reared from galls as primary, larval-pupal, solitary endoparasitoids: *Halticoptera* sp. (Pteromalidae), *Eurytoma* sp. (Eurytomidae), *Torymus* sp. (Torymidae), *Aprostocetus* sp., (Eulophidae), *Brasema* sp. (Eupelmidae) and undetermined species of Platygasteridae and Petromalinae. A gregarious species of *Pronotalia* sp. (Eulophidae) was reared as a primary, larval-pupal, endoparasitoid from galls of *A. trixa*. Some mortality observed in the field was attributed to bird predation on the mature galls.

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